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listen to such arguments and will endeavor to effect improvements.

When such methods fail and the parties interested are obdurate, legal methods should be used. The law or ordinance must be carefully drawn and subjected to the best legal criticism before it is tried. 'It is better never to have sued than to have sued and lost.' But if the ordinance does fail, one has profited by experience and the next ordinance will be stronger.

To sum up the facts and conditions as they have been outlined in this paper it may be said:

(1) That objectionable smoke from soft coal can readily be prevented; (2) that such prevention will result in a higher efficiency and smaller fuel bills; (3) that all new plants should be subject to permits issued by proper city officials; (4) that educational and legal measures combined should be used in cases where the evil already exists; (5) that the control of such work should be in the hands of properly trained engineers who understand the whole subject thoroughly; (6) that the people of each community must see to it that they are protected from this evil as from poor drainage and dirty streets.

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CLEVELAND, OHIO,  
December 15, 1903.

#### *THE CARDINAL PRINCIPLES OF ECOLOGY.\**

WITHIN recent years that old phase of natural history which is concerned with the adaptations of organisms to their environment has become segregated into a distinct department of study under the name of ecology (*œcology*, *biologie*). This separation is unnatural, but it is expedient, and it is likely to result in great advances towards that most important, difficult and

alluring of scientific ends, the explanation of the *raisons d'être* in organic nature.

As now studied by botanists, ecology is concerned mostly with that synthetic phase of the subject dealing with the interpretation of the physiognomy of vegetation, while comparatively little is being done in the analytic phases which investigate particular features, or elements, of adaptation. To such an extent is this the case, in this country at least, that we are accustomed to use the word 'ecology' as a synonym for 'ecology of the vegetation' or 'ecological plant-geography,' a somewhat misleading usage which has been, with some justice, censured. Criticism of the use of the name, however, is of slight account in comparison with the current criticism, unpublished but wide-spread, of the methods of the subject as followed among us. Such criticism arises in part from that ubiquitous human failing which leads us to exalt our own lines of work by invidious reflections upon other lines which we do not, or will not, understand; but it is in large part deserved. Ecological publications in America are too often characterized by a vast prolixity in comparison with their real additions to knowledge, by a pretentiousness of statement and terminology unjustified by their real merits, and by a weakness of logic deserving the disrespect they receive. The subject suffers, I fear, from a phase of the 'get-rich-quick' spirit. These opinions I can express with the better grace when I hasten to admit that, so far as my own few publications are concerned, I am one of the chief of sinners. I believe it is a fact that, despite our numerous ecological publications, the only material advances made in ecology in this country for some years past are in descriptions of vegetation, in which a considerable body of fact has been accumulated. But in interpretation, the very soul of ecology, we have done little

\* Read before the Society for Plant Morphology and Physiology at its Philadelphia meeting, December 29, 1903.

else than continue to kaleidoscope the old and familiar matter. Yet the aim of ecology is perfectly definite, and as lofty as any in science, being nothing less than to explain why each plant is what it is, where it is and in the company it is. Why then do we fall so far behind our ideal? The reason is perfectly plain. We have reached, and long since, the point at which, with our purely observational methods, the law of diminishing return applies strongly to the investigation of the subject; and further substantial advance is now possible only through the aid of some new method. Further, the nature of this new method is equally plain, and it is only practical limitations of time and cost which keep us from utilizing it. It lies in the precise experimental study of the physics of the environment, and of the physiological life histories of particular plants, with the invention of a mode of recording the results in a form to permit the one to be correlated with the other. There must go along with this an improvement in our ecological reasoning; or rather, to be correct, real reasoning, involving logical proof, must be substituted for those speculative yokings of conspicuous effects with prominent possible causes which too often take the place of reasoning in our ecological works.

For this indispensable dual study of environmental physics and adaptational physiology we have some, though no great, foundation. Our knowledge of the physics of the atmosphere and our methods for investigating it are, thanks to meteorology, fairly satisfactory, but we need a new form of record for meteorological data which will make them more directly available than at present in the interpretation of ecological phenomena. Our knowledge of the physics of the soil, however, involving factors more important in the aggregate than those of the atmosphere, is comparatively scanty, while methods for its

exact study are only beginning to be developed. The exact study of soil physics (using this term broadly) seems to me the greatest present single need of ecology. Turning to the other member of the ecological equation, the plant, whose physiological powers and limitations determine its adjustment to particular environments, it appears to be a fact that no attempt has yet been made to apply our considerable physiological knowledge, and our excellent physiological methods, to the elucidation of the physiological life-history of any one of even the important forms constituting our vegetation. Yet it is only through such studies, for which some new appliances and methods must be developed, that we can hope to understand not only the factors involved in the adaptations of the particular form to its environment, but also the nature of the all-important subject of plant-competition, which determines how the forms build up a vegetation. No doubt the subject will ultimately work itself out as a series of ecological life histories, in which the physiological powers and limitations of each plant will be expressed in a system of standard units or formulæ with all the definiteness of the taxonomic terminology of the present day. But such studies as these can not be made by busy teachers who can give to them only a vacation leisure and a scanty equipment. They can be made only by trained investigators who, with ample time, expert assistance, and properly equipped field laboratories, can give themselves wholly to it. Into this fruitful field we welcome the Carnegie Desert Laboratory; may its kind increase until we have not only mountain, jungle, seaside and forest laboratories, but also another form which can be moved from place to place in pursuit of the most pressing problems.

Such seems to me the status of plant ecology at present and the direction it must

take for the future. I propose to discuss now very briefly the principles which appear to me to be fundamental to a right understanding of the nature of ecology.

*Principle 1. The Reality of Adaptation.*—To a first view it seems logically possible that adaptation may have only a subjective existence, and that the cases we consider adaptations may be merely accidental correspondences between certain features of the organism and certain characteristics of the environment, involving no real advantage to the organism. Now there can be no doubt that many cases commonly reckoned as adaptations are of this imaginary nature (it could hardly be otherwise while *post hoc propter hoc* is the prevailing type of ecological reasoning), but that some of our adaptations have an objective existence is susceptible of direct proof. Thus the mechanisms connected with cross-pollination in specialized orchids represent a typical adaptation. If, without other injury to the plant, these mechanisms are prevented from operating, no seed is formed and the result is disastrous to that race of plants. Hence the advantage of the mechanism is made manifest, and the reality of the adaptation is proved.

This case illustrates the fundamental idea, and permits a definition, of adaptation. It is an adjustment between some feature of an organism and some characteristic of its environment such that the organism functions better than it could did such an adjustment not exist.

*Principle 2. The Evolutionary Phylogeny of Adaptation.*—Logically two views are possible as to the phylogeny of a real adaptation. (1) It may have developed quite independently of any connection with the environment it now fits and have come into its present relation with that environment by a sort of sifting process permitted by the constant movement or circulation of organisms in nature, very much as a num-

ber of vari-shaped blocks shaken in a box having vari-shaped cells opening from it would each come finally to fill the cell with which it most nearly corresponds in shape. (2) It may have arisen gradually, either by innumerable fine gradations or by somewhat marked steps, in close touch with the environment, which may be acting either directly causatively or only selectively. The former view has received its strongest advocacy in the recent book by Morgan, while the latter is that almost universally prevailing, and, as I believe, correctly. There is no doubt that some adaptation is of the former sort; and in some phases of ecology, notably in distributional phenomena of ecological plant geography, it plays an important rôle. But that adaptation is usually and essentially of this character seems to me wholly denied by the evidence. There is not, so far as I know, any form of proof that can be adduced to decide between these two possibilities, but there is an argument from probability so strong as to be practically conclusive. It lies in the cooperation of many distinct features of adaptation to fit a form to a very special or unusual environment requiring simultaneous and different kinds of modification in many parts. Thus, to take the case of epiphytes (such as the tropical epiphytic ferns), if these were adapted in but one feature alone, such as the roots, it would be logically quite possible that this kind of root had arisen by some method independent of contact with the environment, and that this form having been brought accidentally into this habitat persists there because these roots fit that environment better than any other. But the probability that this adaptation of the roots has arisen independently of the environment is greatly weakened when we note that so different a structure as the leaves are also, and equally well but in a different way, adapted to this habitat. And when, further, we observe

that adaptations equally good but of a different kind are found in the stems, in the tissue systems, in several phases of irritability and in other features all involving considerable changes from the ancestral forms, then the chances that all of these adaptations, involving most or all of the external structures of the plant, could have arisen without regard to the environment become so small as practically to disappear. On the other hand, the development of adaptations in causative touch with the environment, by whatsoever method the modification may be brought about, gives a perfect explanation of such cases of concomitant adaptations as are here in consideration.\*

Adaptation, as the probabilities overwhelmingly indicate, usually develops in touch with the environment. But from the point of view of the ecologist the method of evolution, whether by selection of fluctuating variations, by inheritance of individually acquired characters, by mutations or by some other method yet unknown, is a matter of only incidental and not of essen-

\* These cooperations of many adaptations fitting a form to a particular habitat, involving changes in many features simultaneously, seem to me to offer one of the very greatest difficulties to the selection theory of the development of adaptations. On the hypothesis of selection of fluctuating variations, favorable variations in one feature bear no relation to favorable variations in another, except in rare cases of correlation. When, therefore, selection is preserving the individuals favorably varying in one character, it is surely preserving unfavorable variations in some other characters. Selection, it would seem, could only produce adaptive modifications in one or a very few characters at a time, and hence simultaneous modifications in many distinct characters, such as actually appear to have occurred in such cases as epiphytes, would not be possible. The mutation theory offers even greater difficulties. The Lamarckian (Neo-Lamarckian) theory, on the other hand, admits of indefinitely numerous concomitant or simultaneous adaptations, though this theory has its difficulties from other points of view.

tial interest. On the other hand, it is altogether likely that adaptation, properly studied, will throw light upon the method of evolution, for it is probably true that adaptation has been in some measure the guide of evolution; or, to express the subject in another way, adaptation seems to bear to evolution a relation somewhat analogous to the relation of a stimulus to its irritable response.

*Principle 3. Adaptation a Race, not an Individual, Process.*—Many phenomena in organic nature point to a distinction between the race and the individuals which compose it. The distinction is not metaphysical but physical, though its precise physical basis is uncertain, the race having its basis in the protoplasm, or the part of it, bearing the characters common to all the individuals, and the individual having its basis in its share of the race protoplasm plus the differences which are its own alone. Now as to the relation of adaptation to race *vs.* individual, two views are possible, aside from any theories: (a) adaptation originates and develops in the individuals, and then, by a method unknown, becomes fixed in the race (a corollary of which is that the individuals are the leading or important element in organic nature, the race being secondary); and (b) adaptation is primarily a race matter, finding its visible expression in the individuals (a corollary of which is that the race is the leading and important element, the individuals being secondary to it). The former is the popular conception and that of some students, but the available evidence seems to point overwhelmingly to the correctness of the second. The phenomena exhibited by the social insects among animals, the regular transmission of both sexes through one sex, and the phenomena of reproduction generally can only be explained on the basis of race adaptation being dominant over individual

adaptation. The distinction often made between adaptations for the good of the individual, such as irritable responses to stimuli, and those for the good of the race, such as various reproductive processes, is merely a matter of convenience without logical basis, for not only is the line between the two extremely indefinite, but also it is evidently as necessary for the good of the race to preserve the reproducing individuals as to secure their reproduction. Adaptation may apparently all be reduced to a race basis, only that being individual which is connected with individual variability. The relation of the race to the individual appears to resemble somewhat the relation of the mortality tables to the individual human life; or the race is like a mighty moving current, while the individuals are the ripples that play upon its surface or the eddies that swirl in its depths. In practice, therefore, adaptation is to be studied from the point of view of its advantage to the race under consideration rather than from the point of view of its individuals; and, further, conclusions can not safely be drawn from individual cases, but must be based upon studies of the race, which can be accomplished best through the use of statistical methods. A corollary of this principle is this, that the meaning of adaptation is to be sought deep in the activities of protoplasm rather than in the superficial manifestations of structure. Structure is but the external manifestation of protoplasmic activity, the tool, as it were, by the aid of which the protoplasm more perfectly accomplishes its work.

*Principle 4. Metamorphic Origin of Adaptation.*—In such cases as I can recall, in which the phylogeny of an adaptive feature is known with reasonable certainty, it seems to be the case that the new adaptation has not arisen *de novo* out of the plant substance, but through the metamorphosis

of some preexistent feature, itself formerly adaptive. It seems to me logically a probability that adaptations frequently, if not generally, have their origins in the metamorphoses of preexisting adaptations, and *omnis adaptatio e adaptatione* may yet become a postulate of ecology. The origin of a new adaptation, upon this principle, would be somewhat after this manner. When changing environmental conditions, or the opening of a new field, bring about a need for a new adaptation, both change and need arising very gradually, this need can be met, and a new adaptation can arise, only in case there is available in the plant some existent feature which happens to be capable of filling that need in its earliest stages, and of being modified to fill it better, either by selection of its fluctuating variations or mutations, or by more direct method, as the need becomes more intense. In such a case, when the full intensity of the need has been reached, the modification or metamorphosis of the original feature will have gone so far that we recognize a new adaptation. If, however, no feature capable of filling the need in its earlier stages exists, or if the need arises too suddenly, then there is no adaptation, the organism can not meet the new conditions confronting it, and it must either keep to its old mode of life, or, if that be impossible, become extinct. Such a principle gives a logical explanation of the remarkable irregularity of distribution of adaptation at the present day, and removes much of the difficulty as to the origin of new adaptations. In discussing the origin of adaptation we too often forget, not only that the need for new adaptations must arise as a rule very gradually, but also that the modifying agency, whatever that may be, makes its effects felt very gradually; or, as it may be expressed, the plant is passed from under the action of one adapting agency to the action of another not

suddenly but gradually. It certainly seems as logical that both adaptations and adaptive agencies should show continuity as that organisms should; and we should be able to trace adaptations back, precisely as we trace organisms, through simpler and simpler conditions until we reach the ultimate origin of them all in the simple undifferentiated protoplasm of the original organisms.

*Principle 5. Inevitable Imperfection of all Adaptation.*—It appears to be true that no feature of any organism is free to respond unhampered to the influence of an agency producing adaptation. Inevitable impediments to such complete responses arise from several sources—from various hereditary influences, from physical and chemical limitations of their powers, from the necessity of providing for nutrition, support and protection, from the presence of other adaptations, and from the presence also, it is possible, of other features highly developed without reference to any utility. The result of the operation of all of these influences upon any feature is a state of equilibrium, of which adaptation is a part, no doubt usually as large a part as the other conditions will permit, but frequently only a minor part. In every case, therefore, adaptation must fall below its perfect development, or must be imperfect. Of no feature can it be true that it is all adaptation, but it must be adaptation plus other considerations, and the latter in any structure may collectively even outweigh the former. Now it is without doubt the task of the ecologist not only to determine adaptation, but as well to delimit the other influences which interoperate with it to make structures what they are. In other words, it is the task of the ecologist to determine the meaning of the features of the plant whether that meaning involves adaptation or not.

Such seems to me the nature of adapta-

tion as indicated by the evidence we possess. Certainly it is true that ecology is but in its beginning. W. F. GANONG.

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#### SCIENTIFIC BOOKS.

PALMER'S 'INDEX GENERUM MAMMALIUM.'\*

DR. PALMER'S 'Index Generum Mammalium' is a work of immense labor, painstakingly and intelligently performed, and its publication will form a landmark in the history of mammalian nomenclature. It furnishes not only an elaborately annotated list of all the generic and family names of mammals, recent and extinct, published since the beginning of the binomial system of Linnæus down to the end of the year 1903, but the introduction, besides disclosing the origin, history and scope of the work, furnishes a fund of historic information that should most favorably influence the methods of the future in the bestowal and use of names by systematists, not only in mammalogy but in other departments of natural history.

The work consists of an 'introduction' of about 70 pages, followed by Parts I.-III., with an appendix, and an index to Part III. Part I. comprises 'Index of Genera and Subgenera' (pp. 71-717); Part II., includes the 'Family and Subfamily Names of Mammals' (pp. 719-776); while Part III. is an 'Index of Genera Arranged According to Orders and Families' (pp. 777-948). The appendix contains names discovered too late to insert in their proper places in Part I. and various additions and corrections, by means of which 'the index is brought down to January 1, 1904.'

In the 'introduction' (pp. 8-69) there is first a statement of the history and purpose of the work. From this it appears that the work was begun by Dr. C. Hart Merriam about

\* 'Index Generum Mammalium: A List of the Genera and Families of Mammals.' By T. S. Palmer, Assistant, Biological Survey. Prepared under the direction of Dr. C. Hart Merriam, Chief of Division of Biological Survey. North America Fauna No. 23, U. S. Department of Agriculture, Division of Biological Survey. Washington, Government Printing Office, 1904. (January 23, 1904.) 8vo, pp. 984.